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Accommodation Without Feedback Suggests Directional Signals Specify Ocular Focus

PHILIP B. KRUGER,*‡ STEVEN MATHEWS,† MILTON KATZ,* KARAN R. AGGARWALA,* SUJATA NOWBOTSING*

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Accommodation was monitored continuously under open-loop conditions while subjects viewed a sinusoidally oscillating sine-wave grating (0.2 Hz; ±1 D; 2.7 c/d; 0.56 contrast) in a Badal optometer. The target was illuminated by monochromatic light (590 nm) or white light (3000 K) with longitudinal chromatic aberration (LCA) normal, doubled, neutralized and reversed. Subjects (12) accommodated well in white light with LCA normal and doubled (mean gains = 0.85 and 0.94), gain was reduced in the neutralized condition (0.54), in monochromatic light (0.43), and especially when LCA was reversed (0.30). The results suggest that accommodation responds to changes in the relative contrast of spectral components of the retinal image and perhaps to the vergence of light.

Accommodation Chromatic aberration Focus Open-loop Stiles–Crawford

INTRODUCTION

Reflex accommodation is modeled routinely as a closed-loop negative feedback system that operates to maximize or optimize luminance contrast of the retinal image (Heath, 1956; Alpern, 1958; Fender, 1964; Toates, 1972; Owens, 1980; Manny & Banks, 1984; Raymond *et al.*, 1984; Kotulak & Schor, 1986; Switkes *et al.*, 1990). In this model both over-accommodation and under-accommodation reduce luminance contrast ($L_{max} - L_{min}/L_{max} + L_{min}$) of the image, and feedback from changes in accommodation is an essential part of the accommodative process. Fincham (1951) disagreed with the notion of an "even-error" stimulus without directional quality, and proposed "odd-error" directional signals from chromatic aberration and the angle of incidence of light reaching directionally sensitive cones (Stiles–Crawford effect). Fincham (1951) noted that small eye movements initiate reflex changes in accommodation, and postulated that oblique viewing as a result of the eye movements, together with the waveguide property of cones, produce a "difference of brightness stimulus" between the two sides of the blur circle. In Fincham's model the "bright" side of the blur circle (the peak of the "effective" intensity distribution) changes from one side of the blur circle to the other side as focus changes from behind to in front of the retina. The method relies on small off-axis eye movements (<10 arc sec) and assumes that the peak of the Stiles–Crawford function is at the center of the pupil.

An effect similar to that described by Fincham occurs without the need for off-axis eye movements if the peak of the Stiles–Crawford function is decentered toward one side of the pupil (Westheimer, 1968). The peak of the Stiles–Crawford function often is decentered by a small amount (0.5 mm), usually in the nasal direction (Stiles & Crawford, 1933; Enoch, 1957; Applegate *et al.*, 1987; Gorrand & Delori, 1995) and some eyes have markedly decentered Stiles–Crawford functions (e.g. Westheimer, 1968). The principles of the present method for determining focus are illustrated in Fig. 1 for a centered pupil and an aberration-free optical system. To simplify the description, angle alpha (between the optic and visual axes) is not included. An array of retinal receptors are shown with all the receptors facing toward the left side of the pupil. Cones gather light over relatively small acceptance angles (Makous, 1977; Enoch *et al.*, 1977; Bailey & Heath, 1978; Enoch & Lakshminarayanan, 1991) so that in this example light incident from the left side of the pupil is more effective for stimulating the receptors than light incident from the right side of the pupil. Although the blurred intensity distribution on the retina is symmetrical in this example, the peak of the *effective* intensity distribution (the neural representation of the intensity distribution after the Stiles–Crawford effect) is skewed to the left in the case of under-accommodation, and to the right in the case of over-accommodation. The direction of asymmetry specifies focus behind or in front of the retina. Several lines of evidence suggest that the retinal image is represented at an early stage of visual processing by spatial "primitives"

*Schnurmacher Institute for Vision Research, State College of Optometry, State University of New York, New York, NY 10010, U.S.A.
†Texas Tech University Health Science Center, Department of Ophthalmology, Lubbock, TX 79430, U.S.A.
‡To whom all correspondence should be addressed.

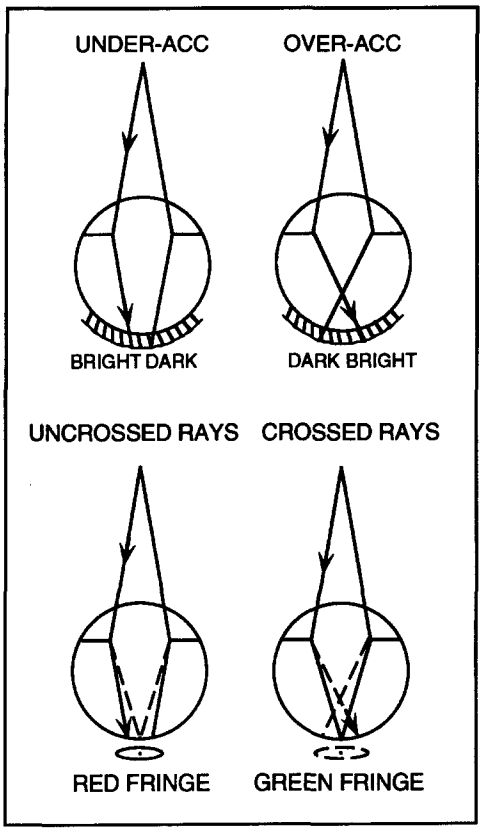

FIGURE 1. Illustration of proposed achromatic and chromatic directional signals from the angle of incidence of light and a decentered Stiles–Crawford function (top) and from chromatic aberration (bottom). The top illustration is for an aberration-free optical system with a small (3 mm) pupil. When the pupil is larger, the presence of positive spherical aberration prevents the abrupt change from crossed to uncrossed rays because peripheral rays converge to focus ahead of paraxial rays.

such as peaks, centroids and zero-crossings in the second derivative of the retinal intensity profile (Marr *et al.*, 1979; Marr & Hildreth, 1980; Watt & Morgan, 1983; Toet *et al.*, 1988; Morgan, 1991; Ye *et al.*, 1992). If the peak of the effective intensity profile changes position systematically with changes in focus this could provide a signal that indicates focus.

The proposed method for determining focus (decentered Stiles–Crawford function) is presented as an heuristic, and to illustrate the optical principles, however, foveal cones might identify focus by other methods. A primary issue is whether foveal cones all face toward the same point in the exit pupil, or whether there is some degree of receptor disarray that allows individual foveal cones or groups of cones to sample from circumscribed areas of the pupil (Makous, 1977; Safir & Hyams, 1969; Coble & Rushton, 1971; Snyder & Pask, 1973; MacLeod, 1974; Enoch *et al.*, 1977; Bailey & Heath, 1978; Enoch & Lakshminarayanan, 1991). Williams (1980) concluded that some of the light falling within the central 2 deg of the fovea is refracted by the sloping walls of the foveal pit, and as a consequence, cones in a small annular area around the central fovea sample light from areas of the pupil that are displaced radially from the pupil center. Cones on the left side of the fovea sample from the left side of the pupil, while cones on the right side of the fovea sample from the right side of the pupil. By application of the Scheiner principle, comparison of signals from opposite sides of the pupil could provide a measure of focus.

A related consideration is that light propagates along retinal cones in patterns called modes (Toraldo di Francia, 1949; Enoch & Lakshminarayanan, 1991). Modal patterns are an interference phenomenon that occurs when light is incident along the axis of thin optical fibers that have diameters close to the wavelength of light (Wijngaard, 1974). The modal patterns that are propagated vary both as a function of the wavelength of light, *and* the angle of incidence of light, and several modes can be propagated simultaneously. Enoch (1961) observed modal patterns in several species, and noted that the propagated modes varied as a function of the position of the focal plane within the receptor. Enoch (1961) also noted that in monochromatic light some receptors "change mode patterns abruptly at a well-defined wavelength" while in white light "the terminals of the receptors light up with overlapping colored patterns" (Enoch & Tobey, 1981). At the leading edge (tail) of the polychromatic blur spread-function, the angle of incidence and the wavelength of light vary systematically as a function of changes in focus, and the modal patterns that are propagated also vary "when the focal plane within the receptor is varied" (Enoch, 1961). The notion that the eye might be sensitive to the vergence of light remains speculative, and further investigation is warranted.

Besides any role that the waveguide nature of cones might play in determining focus, an optical signal could result from a decentered pupil and from asymmetric monochromatic aberrations (Collins *et al.*, 1995). In an aberration-free eye the peak of the point spread-function is decentered in the same direction as the decentered pupil in the case of over-accommodation, and in the opposite direction in the case of under-accommodation. In addition, eyes with large pupils (>3 or 4 mm) have spherical aberration that often is asymmetric across the area of the pupil (Walsh & Charman, 1985), and coma produces a lateral shift of the peak of the point spread-function when focus changes that might provide a directional signal (Walsh & Charman, 1989). Psychophysical measurements of ocular aberrations (Howland & Howland, 1977; Campbell *et al.*, 1990) and recent double-pass measurements of retinal image quality (Artal *et al.*, 1995) suggest that considerable asymmetric (coma-like) aberration can be present at the fovea. The effects of aberrations and a decentered pupil can interact with a decentered Stiles–Crawford function (Ye *et al.*, 1992; Rynders *et al.*, 1995) and the resulting signal might specify focus.

Fincham (1951) also proposed a chromatic signal from the effects of longitudinal chromatic aberration (LCA) of the eye, as illustrated at the bottom of Fig. 1. Long-wavelength light comes to focus further back in the eye than short-wavelength light, producing color fringes

around the images of polychromatic points of light and at edges. Under- and over-accommodation produce red and blue fringes, respectively, and the color of the fringe specifies the direction of defocus. Another method of describing the chromatic signals is in terms of the contrast ($L_{max} - L_{min}/L_{max} + L_{min}$) of spectral components of the image (Marimont & Wandell, 1994; Kruger *et al.*, 1995a). Contrast of the retinal image is maximum for the spectral component of the image that is in focus, and contrast is reduced for spectral components focused behind and in front of the retina. At low spatial frequencies (<0.5 c/d) defocus and aberrations have little or no effect on contrast of the image, but at higher spatial frequencies defocus reduces luminance contrast, and LCA alters the contrast of spectral components (e.g., red, green and blue) of the image. The chromatic effects are prominent at intermediate spatial frequencies (3–5 c/d) and very large at higher spatial frequencies (>10 c/d). Figure 1 (bottom) shows that under-accommodation is characterized by higher contrast for the short-wavelength (in-focus) component of the retinal image than the long-wavelength (under-focused) component, and over-accommodation is characterized by higher contrast for the long-wavelength component than the short-wavelength component. Thus, the relative contrast of spectral components of the retinal image specifies focus behind or in front of the retina. The diagrams at the bottom of Fig. 1 also show that the "achromatic" signal, perhaps from the angle of incidence of light, and the chromatic signal from LCA are closely related. In the case of over-accommodation, the short-wavelength rays of light that produce the green color-fringe come from the opposite side of the pupil (rays entering the eye on the left side of the pupil "cross" at focus to form the right side of the blur circle). In the case of under-accommodation the long-wavelength rays that produce the red fringe come from the same side of the pupil and are "uncrossed", in that light entering near the left pupillary margin forms the left edge of the blur circle. Under normal conditions there is a close correlation between the wavelength of light that forms the margin or tail of the edge spread-function and the angle of incidence or direction of light that forms the colored fringe.

In the present experiment an attempt is made to minimize the effects of monochromatic aberrations by using a 2.7 c/d sine-wave grating as the accommodation target, and by imaging a 3 mm artificial pupil close to the visual achromatic axis of the eye. The effect of monochromatic aberrations on contrast of the retinal image is negligible below 3 c/d if the target is viewed through a 3 mm pupil. Accommodation is driven by changing target vergence in the absence of blur feedback (electro-optical open-loop) with the target illuminated by narrowband monochromatic light to test for the presence of an achromatic directional stimulus, and with the target illuminated by broadband white light, with LCA doubled, normal, neutralized and reversed to examine the contribution of the proposed chromatic stimulus (chromatic difference of contrast). Entoptic viewing of the Stiles–Crawford effect (Westheimer, 1968) is used to determine whether subjects who accommodate well in monochromatic light also have markedly decentered Stiles–Crawford functions.

Following the prevailing model of accommodative control (luminance contrast-decrement provides the stimulus and negative feedback is a necessary part of the process) subjects should not be able to accommodate effectively under open-loop stimulus conditions. On the other hand, if reflex accommodation responds to odd-error chromatic information, subjects should accommodate well in the presence of chromatic aberration (normal and doubled), the response should be impaired in the absence of chromatic aberration (neutralized and monochromatic), and in the reversed condition subjects should track in counterphase to the target motion (accommodation should respond in the wrong direction). In addition, if reflex accommodation responds to odd-error achromatic information, subjects should accommodate in monochromatic light in the absence of feedback. Finally, in the reversed condition the usual linkage between the relative contrast of spectral components of the retinal image (proposed chromatic signal) and the angle of incidence of light (proposed achromatic signal) is disturbed, and the chromatic and achromatic signals change in temporal counterphase to each other during the experiment. If both chromatic and achromatic directional stimuli drive reflex accommodation the stimuli should counteract each other in the reversed condition.

METHODS

Accommodation was monitored continuously by an infrared recording optometer, while subjects viewed a sine-wave grating target in a Badal stimulus system. The infrared optometer operates over a range of 8 D, resolution is better than one-tenth of a diopter, and the cut-off frequency is 10 Hz. The optometer is insensitive to eye movements up to 3 deg from the center of the target, and operates with a pupil size of 3 mm in diameter or larger (Kruger, 1979). Mydriatics were not used to dilate the subjects' pupils.

The essential components of the stimulus system are shown in Fig. 2. The stimulus system is a modified Badal optometer (Crane & Cornsweet, 1970) that allows the stimulus to accommodation (dioptric vergence) to be varied sinusoidally without changing the visual angle subtended by the target (Ogle, 1968). The grating target is presented in white light (3000 K) or monochromatic light (550 nm with 10 nm bandwidth) at a mean luminance of 200 cd/m^2. Neutral density filters are used to match target luminance in monochromatic and white light. The target (T) is a 2.7 c/d vertical sine-wave grating* with Michelson contrast ($L_{max} - L_{min}/L_{max} + L_{min}$) of 0.56.

*The grating was photographed from a Tektronix 602 oscilloscope. Negatives were produced on Kodak RAR 2498 film and developed for a gamma of 0.6. Positives were made from the negatives on Kodak Fine Grain Release Positive 5302 and developed so that the product gamma of negative–positive was 1.0.

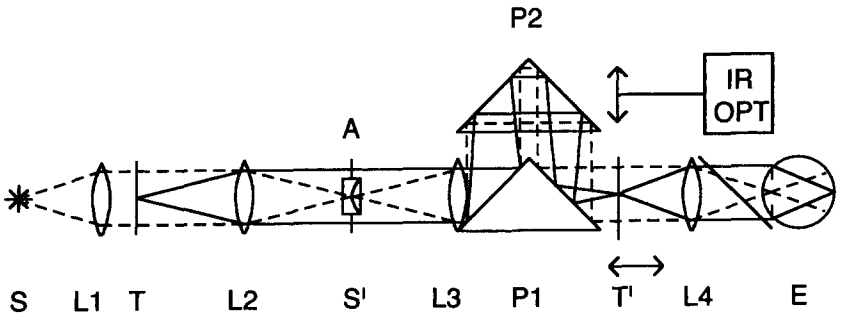

FIGURE 2. Instrumentation includes an infrared optometer (IR OPT) for monitoring accommodation and a Badal stimulus system and servo-mechanism for stimulating accommodation and producing the open-loop condition. Two superimposed optical systems include an illumination system (dashed lines) and a target system (solid lines). Light from the source S is collimated by L1 and brought to focus by L4 in the pupil of the subject's eye E. Aperture A is also imaged in the pupil of the eye. Output of IR OPT controls position of prism P2 and position (vergence) of target image T'.

The grating subtends 6 deg at the eye and is surrounded by a blurred circular field stop (6 deg) positioned 8 D beyond optical infinity. Prism P2 can be moved, as shown by the arrow, to alter the distance between the image of the target (T') and Badal lens L4. The position of prism P2 is controlled by a servo-motor and computer that produce sinusoidal changes in the position of the target image. When T' is in the focal plane of L4, light from the target is collimated by L4 and focused on the retina of the (emmetropic) eye. Reflex accommodation is driven by moving the target sinusoidally toward and away from Badal lens L4. This alters the vergence of light reaching the eye from the target and stimulates reflex accommodation. The infrared optometer operates off a hot mirror positioned between the Badal lens and the eye. Output of the infrared optometer is recorded by polygraph and sampled at 100 sec^{-1} by computer.

The chromatic aberration of the eye can be altered by positioning one of three specially designed lenses at aperture A. The lenses are cemented doublets made of crown (SK16 620603) and flint glass (F2 620364) with plano front and back surfaces. The radii separating the crown and flint components of the doubling, neutralizing and reversing lenses are 117, −105 and −54 mm, respectively. The lenses have zero power at 588 nm and appropriate power at shorter and longer wavelengths to double, neutralize or reverse the normal longitudinal chromatic aberration of the eye. The effect of the three lenses on LCA is shown in Fig. 3, together with data for normal chromatic aberration. The measures of normal chromatic aberration are similar to those of Bedford & Wyszecki (1957). The doubling lens substantially increases the aberration at each wavelength and the reversing lens reverses the lens power needed to correct the aberration at each wavelength. The neutralizing lens focuses most wavelengths of light in the same plane in the eye, but under-corrects LCA by a small amount (approx. 0.3 D) above approximately 600 nm. Thus, the neutralizing lens minimizes chromatic aberration but does not completely eliminate the aberration (chromatic aberration is reduced from approx. 1.5 D to approx. 0.3 D between 450 and 670 nm). Control experiments show that the zero-power doublets do not alter contrast

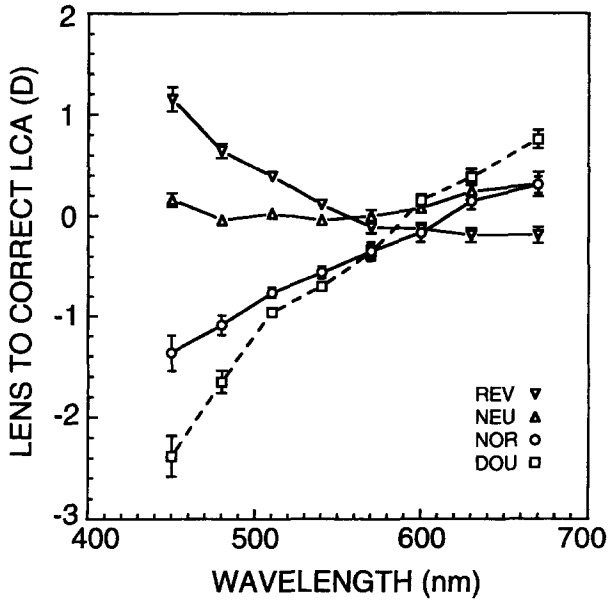

FIGURE 3. Chromatic difference of focus (LCA) for six subjects measured through the stimulus system with and without the reversing, neutralizing and doubling lenses in place.

sensitivity of the eye (Kruger *et al.*, 1993) or depth of focus of the eye (Mathews *et al.*, 1994).

The open-loop condition is achieved by feeding the voltage signal from the infrared optometer (accommodative response) to the computer-controlled servo-system that controls the position of the target in the Badal optometer. Using this method, changes in focus of the eye are compensated by equivalent changes in dioptric vergence of the target, and the retinal image is fixed along the z-axis of the eye. In the open-loop condition changes in accommodation have no effect on the clarity (contrast) of the retinal image because blur feedback is eliminated. Unlike other methods of eliminating blur feedback (e.g. use of a pinhole to provide a large depth of focus) the present method allows stimulation of accommodation by defocus blur (changes in target vergence) in the absence of feedback, with a normal (3 mm) pupil aperture. In addition to the standard open-loop condition (zero feedback), small amounts of negative or positive

feedback can be introduced by altering the gain of the signal from the infrared optometer to the servo-mechanism that controls target distance (vergence). The position of the image in the subject's eye also can be offset by a small amount (e.g. 0.1, 0.2 D) with respect to the retina under computer control. The frequency response of the optometer and the servo-system that eliminates blur feedback has been described previously (Kruger *et al.*, 1995a). Gain is relatively constant across temporal frequency (0.05–2 Hz), and phase-lag increases gradually with temporal frequency. The response of the optometer and servo-mechanism are fast enough to ensure an accurate open-loop condition at 0.2 Hz (the frequency of target motion in the present experiment) and at high temporal frequencies (2 Hz) there is a small phase-lag (30 deg) that precludes a perfect open-loop condition. Small rapid oscillations of accommodation occur at frequencies up to 2 Hz, however, the lower frequency oscillations of accommodation (<0.6 Hz) are more likely to be involved in accommodative control than high-frequency oscillations (Charman & Heron, 1988; Winn *et al.*, 1989; Denieul & Corno-Martin, 1994).

The target in the present experiment (2.7 cpd sine-wave grating) was chosen because dynamic accommodation responds best at intermediate spatial frequencies (3–5 cpd) and the effects of LCA on accommodation are prominent at 3 cpd (Stone *et al.*, 1993; Mathews & Kruger, 1994). In addition, when the present target is viewed through a 3 mm pupil, the effect of monochromatic aberrations is negligible on spatial contrast and phase of the image. The present stimulus conditions minimize monochromatic aberrations (spherical aberration and coma) that might contribute to the stimulus at higher spatial frequencies and for larger pupil sizes.

Procedures

Control experiments. Several control experiments were run to examine the effects of the zero-power doublets on the retinal image. Longitudinal chromatic aberration, transverse (lateral) chromatic aberration, and contrast sensitivity were measured through the Badal stimulus system with and without the lenses in place. The methods used in these control experiments have been described previously (Kruger *et al.*, 1993). In short, LCA was measured under cycloplegia using a procedure similar to that of Howarth & Bradley (1986). Subjects (five) used a potentiometer control and the method of adjustment to focus a Maltese cross target illuminated by eight monochromatic lights between 450 and 670 nm. Transverse chromatic aberration (TCA) also was measured under cycloplegia. Subjects (six) aligned vertical red (650 nm) and blue (470 nm) vernier line targets using the method of adjustment while viewing the vernier targets foveally in the Badal optical system. Contrast sensitivity was measured using a two-alternative (spatial) forced-choice procedure. Subjects indicated by key-press whether vertical gratings appeared in the left or right half of the stimulus field (Stone *et al.*, 1990; Kruger *et al.*, 1993).

Accommodation experiment. A bite plate and forehead rest helped the subject remain still, the right eye was patched, and trial lenses before the left eye compensated for any ametropia. The room was dark and the target was the only visible stimulus. The left eye of the subject was aligned with the apparatus using a telescope to focus and align the corneal reflection of the target (Purkinje image I). The present method of alignment positions the first Purkinje image (PI) at the center of the artificial pupil and this positions the visual (achromatic) axis of the eye close to the optic axis of the stimulus system.

Calibration of the accommodative response was performed at the beginning of each experimental session. For the calibration procedure the grating target was replaced with a high-contrast white Maltese cross to ensure an optimal accommodative response. The subject was instructed to keep the target clear as it stepped through 0, 1, 2, 3 and 4 D of accommodative demand, pausing for 8 sec at each dioptric level. The accommodative response to the five stimulus levels was displayed on the computer screen, the average responses to the 1 and 3 D stimulus levels were estimated from the display, and these measures were used to scale the signals for the open-loop condition and for subsequent data analysis. The method provides an absolute calibration of accommodation only if the subject accommodates accurately for the 1 and 3 D stimulus levels. Under the present stimulus conditions subjects accommodate accurately to the 1 D stimulus, but they tend to under-accommodate by a small amount (e.g. 0.25 D) to the 3 D stimulus. Such under-accommodation during the calibration procedure can result in a small amount of positive feedback (e.g. +0.1) in the nominally open-loop condition.

Following the calibration procedure, the cross target was replaced with a grating target positioned in the optometer to provide 2 D of stimulus to accommodation. The subject was instructed to "concentrate on the center of the target", and once the subject was accommodating accurately to the stationary stimulus, the open-loop condition was initiated by a keypress. In the absence of feedback, accommodation becomes unstable and sometimes drifts toward the near point of accommodation (e.g. 8 D) or toward optical infinity (0 D). Such drift could be minimized if necessary by introducing a small amount of defocus offset (e.g. ±0.1 D) behind or in front of the retina, to stabilize accommodation. The ability to introduce small amounts of defocus offset under computer control before the beginning of the trial made it possible to record for the duration of a 40-sec trial from a few subjects who otherwise would accommodate beyond the dynamic recording range of the system (0–7 D). Once it was clear that accommodation had stabilized under open-loop control, sinusoidal target oscillation was initiated. The target first moved away from the eye (target moved in front of the retina) and data collection for the 40-sec trial began a few seconds later when the target image was 1.0 D behind the retina.

There were five stimulus conditions: (1) doubled (white light with twice the normal amount of chromatic aberration); (2) normal (white light with the usual amount

of chromatic aberration); (3) neutralized (white light with chromatic aberration largely eliminated); (4) reversed (white light with chromatic aberration opposite to normal); and (5) monochromatic (green target of 550 nm without effects of chromatic aberration). The five conditions were presented in random order to each subject, and six trials of 40 sec duration were run for each condition. Output of the infrared optometer was sampled by computer at 100 sec^{-1}, blinks were removed in "real-time", data were scaled according to the calibration, and the accommodative response was fed to the servo-system that controlled the position of the target along the z-axis. The accommodative response was summed with a sinusoidal signal from the computer (2 D amplitude at 0.2 Hz) so that the grating image formed in the subject's eye moved sinusoidally from 1 D behind the retina to 1 D in front of the retina, regardless of the accommodative response. After each 40-sec trial the data were analyzed by fast Fourier transform to estimate the amplitude and phase of the accommodative response at 0.2 Hz. Gain (amplitude of response divided by amplitude of stimulus) and phase-lag (degrees from stimulus peak to response peak) for the six trials for each condition were vector-averaged to provide mean gain, phase-lag, and standard errors for each condition.

One subject (S4) was examined in detail to determine whether a small amount of residual feedback might account for the strong open-loop response of this subject in monochromatic light. Trials were run with feedback gain set at −1.0 (closed-loop normal, negative feedback), −0.5 (half the usual amount of negative feedback), −0.2, 0 (open-loop with no feedback), +0.1, +0.2, +0.3 and +0.4 (positive feedback). The trials with small amounts of positive feedback (e.g. +0.1) tested the possibility that a small amount of residual negative feedback (e.g. −0.1) from an inaccurate calibration might be responsible for the open-loop response.

Finally, three subjects who responded well in monochromatic light (S4, S7 and S10) were examined to determine whether their Stiles–Crawford functions were centered or decentered to one side of the pupil. A simple method for viewing the Stiles–Crawford effect entoptically was described by Westheimer (1968). The method relies on a subjective description of the intensity distribution (brightness) across a defocused blur circle. If the foveal cones point toward the center of the pupil, the defocused blur circle appears brightest at the center, but if the cones point to one side of the pupil, the defocused blur circle appears brighter on one side and darker on the opposite side (Fig. 1). The bright and dark sides of the blur circle switch sides as focus changes from myopic to hyperopic. In the present application of the method subjects viewed a small light source monocularly at a distance of 4 m through their distance lenses (if any) and with natural pupils. Trial lenses (+8 or −8 D spheres) were positioned before one eye to produce a large defocused blur circle on the retina, and the subject was asked to describe and draw the appearance of the blur circle for the two conditions of defocus.

Subjects

Twelve subjects between the ages of 22 and 43 yr participated in the accommodation experiment, and several additional subjects took part in control experiments. Subjects had sufficient amplitude of accommodation for the experiment, they were free of ocular pathology, had 20/20 Snellen visual acuity, and normal color vision (anomaloscope). One subject (S4) was deuteranomalous, and all subjects gave informed consent.

RESULTS

Control experiments

The effects on LCA of the doubling, neutralizing and reversing lenses are shown in Fig. 3 (mean of five subjects) together with a plot for normal LCA. The doubling lens increases LCA from approximately 1.75 D in the normal condition to almost 3.0 D in the doubled condition. The neutralizing lens eliminates LCA between 450 and approximately 580 nm, it under-corrects for longer wavelength light, and over-corrects by a small amount for short wavelength light. The residual chromatic aberration for long-wavelength light is approximately 0.3 D and this small amount may be sufficient to assist reflex accommodation for some subjects (Kruger *et al.*, 1995b). Thus, it is more accurate to consider the neutralizing lens a "reducing" lens, in that it does not entirely eliminate LCA. In contrast to the neutralized condition, the effects of LCA are completely eliminated in the monochromatic condition. The reversing lens was designed to over-correct the normal LCA of the eye so that when middle wavelength light is in focus, short-wavelength light focuses behind the retina rather than in front, and long-wavelength light focuses in front of the retina rather than behind. The lens operates essentially as designed, although the total amount of LCA between 450 and 670 nm is less in the reversed condition (1.3 D) than in the normal condition (1.7 D).

The effect of the lenses on transverse (lateral) chromatic aberration (TCA) is shown for six subjects in Table 1. Without the special lenses in the Badal stimulus

TABLE 1. Transverse chromatic aberration for six subjects measured in arc sec

S#	Normal	Neutral	Doubled	Reversed
1	15 ± 12	43 ± 13	75 ± 09	112 ± 24
2	68 ± 21	94 ± 60	185 ± 32	90 ± 89
4	16 ± 20	28 ± 22	99 ± 27	97 ± 37
14	50 ± 27	40 ± 14	75 ± 30	111 ± 16
15	46 ± 38	95 ± 12	21 ± 37	122 ± 71
16	−73 ± 57	−17 ± 18	−41 ± 31	44 ± 38
Mean	20.3	47.2	69.0	96.0
SEM	±20.5	±17.3	±31.0	±11.4

Subjects 1, 2 and 4 participated in the open-loop accommodation experiment. Subjects 14, 15 and 16 participated in closed-loop experiments that were run at the same time as the open-loop experiment, and complete open-loop data sets were not collected from these subjects. Their closed-loop data are much like the open-loop data of subjects 1 and 2 in the present experiment.

system, TCA ranges from +68 to −73 sec arc with a mean of +20 sec arc. These measures of TCA are similar to TCA measured without the intervening optical system (Ogboso & Bedell, 1987; Simonet & Campbell, 1990; Thibos *et al.*, 1990; Rynders *et al.*, 1995). Mean TCA for the six subjects is +47 sec arc through the neutralizing lens, +69 sec arc through the doubling lens, and +96 sec arc through the reversing lens. The mean measures increase by approximately 25 sec arc for each successive lens condition (normal to neutralized to doubled to reversed) but there are individual differences in this pattern among the six subjects. Subject S2 shows twice as much TCA in the doubled condition than in the neutralized or reversed conditions, and S4 shows a similar amount of TCA in the doubled and reversed conditions. The doubling lens generally increases TCA, but has no adverse effect on dynamic accommodation; thus the doubled condition provides a control for the possibility that induced TCA is responsible for impaired accommodation in the neutralized and reversed conditions.

Accommodation experiment

Accommodation becomes unstable in the absence of negative feedback, and focus of the eye tends to drift toward the subject's individual resting position of accommodation. A few subjects over-accommodated persistently as if in accommodative spasm (e.g. 6 D or more), and a few accommodated persistently for optical infinity (0 D). However, the majority of subjects could maintain focus within the preferred recording range (0.5–6 D) for a period of 60 sec. Three subjects required small amounts of defocus offset (e.g. 0.1–0.3 D) to maintain their accommodation between 0.5 and 6 D. Two subjects were rejected after initial screening because of persistent over-accommodation (e.g. 7 D) that could not be stabilized by defocus offset, and one subject was rejected for persistent accommodation for distance (0 D) in the open-loop condition. Persistent over- or under-accommodation produces truncated accommodation responses to the sinusoidally moving target, because the near-point or far-point of accommodation restrains the response (the top or bottom half of the sinusoidal response is missing). In general, it was unnecessary to stabilize accommodation with defocus-offset.

To illustrate the sequence of events leading up to each 40-sec open-loop trial, Fig. 4 shows three curvilinear pen-traces that were recorded simultaneously. The records include a 15-sec stationary period before the beginning of the experimental trial, during which time the closed-loop condition changed to the open-loop condition. A vertical arrow at the bottom of Fig. 4 indicates when accommodative control changed from closed-loop to open-loop. The top trace represents the stimulus to accommodation in diopters under the open-loop condition, and is the voltage signal from the computer to the servo-mechanism that controls target distance (vergence). At the beginning of the recording period the target remained stationary for several seconds following initiation of the open-loop

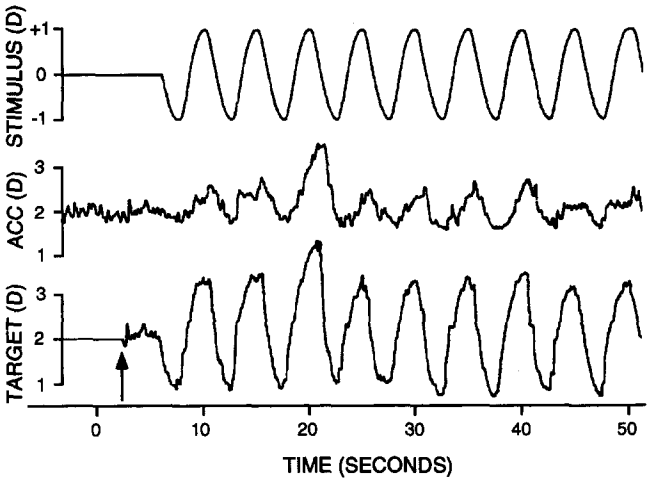

FIGURE 4. Dioptric stimulus to accommodation (top trace), closed-loop followed by open-loop accommodative response (middle trace), and target position (bottom trace). Vertical arrow indicates when control changed from closed- to open-loop.

condition. The middle trace is the accommodation response (voltage signal from the infrared optometer). Accommodation remained relatively stable while the subject viewed the stationary target first under closed-loop and then open-loop control. Once target motion started, accommodation followed the target with a phase-lag of approximately 80 deg. The bottom trace is the sum of the signal from the infrared optometer (middle trace) and the stimulus signal from the computer (top trace), and this combined signal controlled the position of the target (T′ and prism P2 in Fig. 2) during the open-loop condition. Data in Fig. 4 were recorded during a single monochromatic trial.

It became clear early in the study that subjects accommodate readily in the absence of negative feedback, especially in broadband white light. Figure 5 shows accommodation data from four subjects for one trial of each condition to illustrate the range of responses presented by the 12 subjects. For each set of data the top trace represents the sinusoidal dioptric stimulus, and the traces below are responses to the five experimental conditions. All four subjects responded well in the normal and doubled conditions, but there are differences in their responses to the other conditions. The responses of the first two subjects (S1 and S2) to the five experimental conditions are typical, except that one subject responded with lower gain than the other. The two subjects accommodated well in the normal and doubled conditions, the response was reduced in the neutralized and monochromatic conditions, and there was little or no response in the reversed condition. Subject S3 shows the same pattern, but in the reversed condition the response was in temporal counterphase to the stimulus. The counterphase response suggests high sensitivity to the chromatic stimulus combined with low sensitivity to the achromatic stimulus. Subject S4 responded well in the absence of LCA (neutralized and monochromatic conditions) and responded with reduced gain but normal phase-lag in the reversed condition.

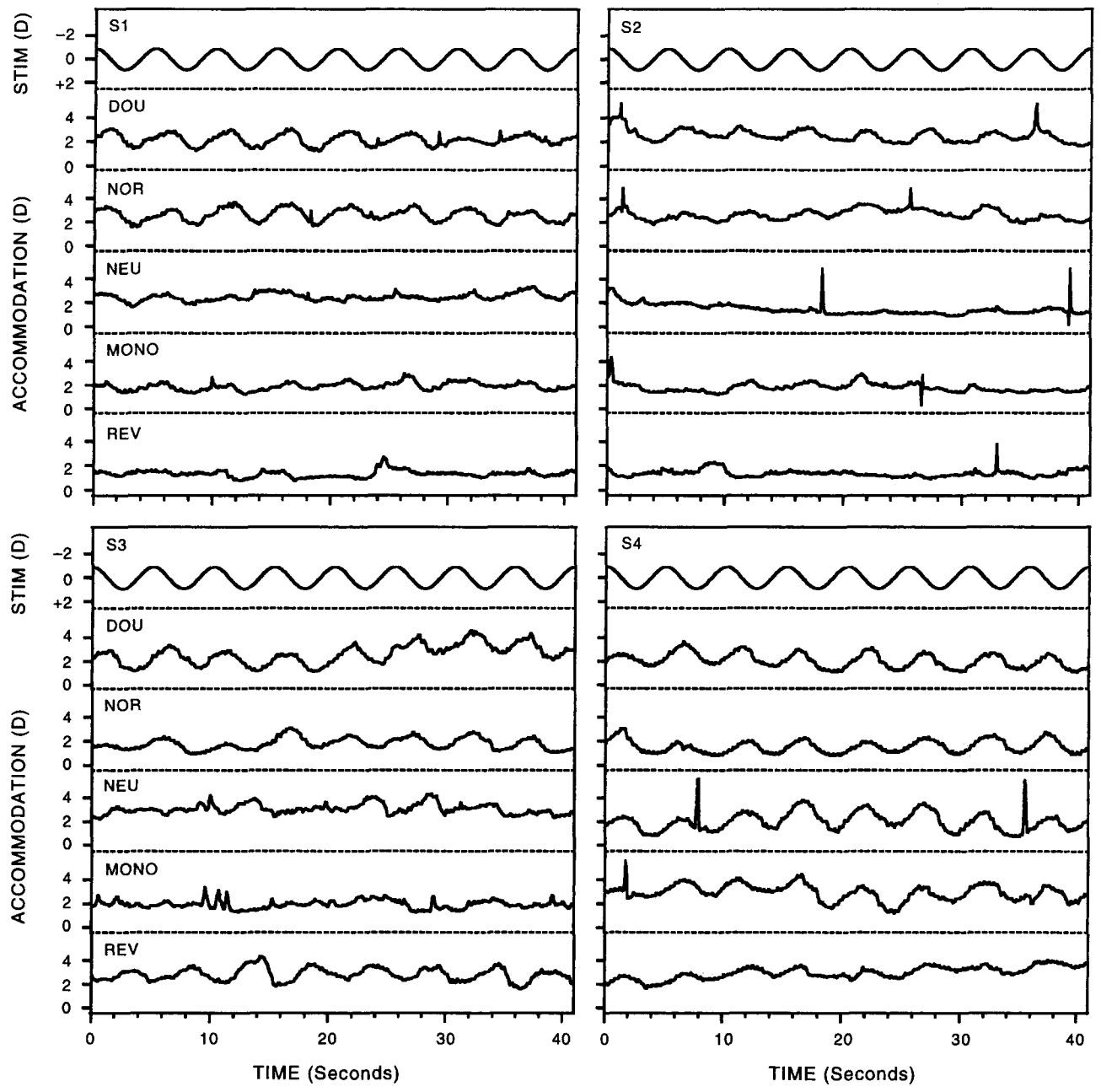

FIGURE 5. Data for single 40-sec trials from four subjects for five experimental conditions.

Figures 6 and 7 present the mean gain and phase-lag of accommodation for each condition for all 12 subjects. The effect of the five LCA conditions on gain provides an index of the subject's sensitivity to the chromatic stimulus. For most of the subjects, gain is highest in the normal and doubled conditions (mean gains = 0.85 and 0.94, respectively), gain is reduced in the neutralized and monochromatic conditions (means = 0.54 and 0.43), and gain is small or absent in the reversed condition (mean = 0.30). It is clear that some subjects are more sensitive than others to the effects of LCA. Some subjects responded with higher gain in the doubled condition than the normal condition (e.g. S8, S9, S11) but for most subjects doubling the amount of LCA had no effect. Phase-lag varied between 60 and 90 deg depending on the subject, and phase-lag remained approximately the same for the five conditions. One subject (S3) responded in temporal-counterphase in the reversed condition on all six trials, and three subjects (S6, S11, S12) responded in counterphase on three out of six trials, although with very low gain.

Additional trials were run on subject S4 in monochromatic light to test the possibility that a small amount of residual negative feedback might account for the open-loop response. Vector-averaged gain and phase data are presented in Table 2 for feedback values from −1.0 to +0.4. As the normal amount of negative feedback was reduced in steps from −1.0 to zero, gain increased by a small amount, and phase-lag increased substantially. Gain was not adversely affected by the absence of feedback at 0.2 Hz, but phase-lag increased as feedback was eliminated. On the other hand, as positive feedback

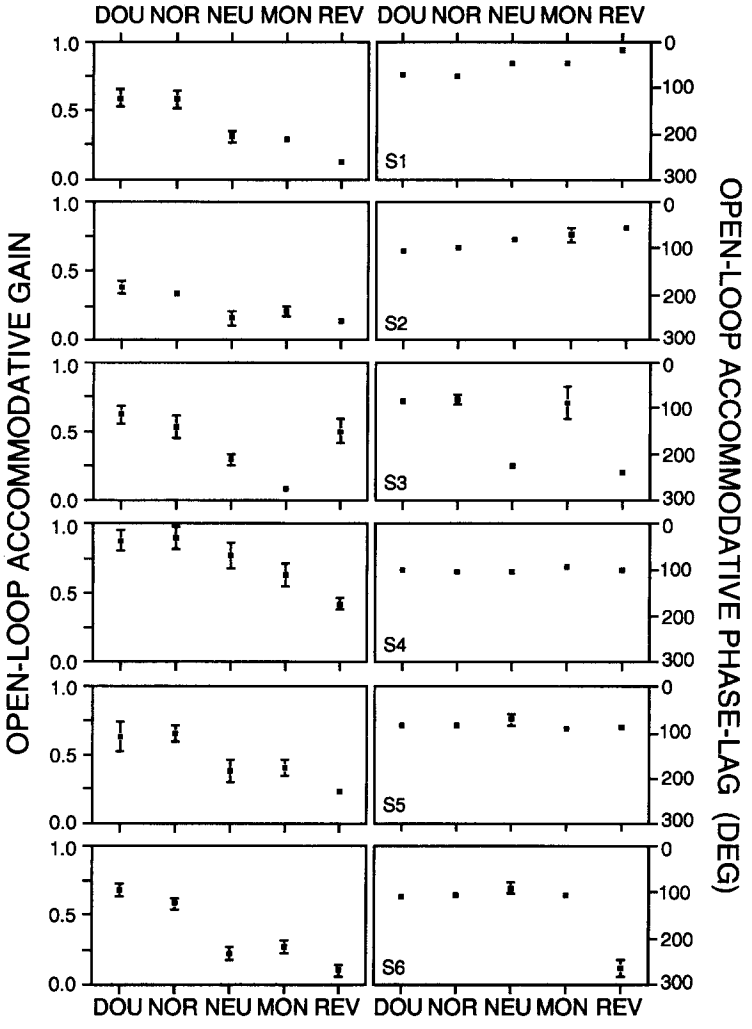

FIGURE 6. Gains (left) and phase-lags (right) for six subjects with low to moderate gains.

was introduced in small steps, gain decreased and phase-lag remained approximately the same (approximately 100 deg). In addition, under open-loop control small amounts of defocus offset (0.2 D) behind or in front of the retina of this subject were sufficient to drive accommodation in the appropriate direction while the subject was viewing a stationary target.

Univariate analysis of variance for a repeated measures design was run on the gain data for 12 subjects. The F-test was significant ($F = 20.93$; $P < 0.001$) and a subsequent multiple comparison test (Scheffe) showed that the normal condition was significantly different from the neutralized condition ($P < 0.05$) as well as from the monochromatic condition ($P < 0.01$) and the reversed condition ($P < 0.01$). The normal and doubled conditions were not significantly different ($P > 0.05$), and the neutralized and monochromatic conditions also were not significantly different ($P > 0.05$).

Entoptic viewing of the Stiles–Crawford effect was performed by three subjects who responded the best in monochromatic light (S4, S8 and S10). Subjects S4 and S10 described a pronounced asymmetry in the brightness of the defocused blur circles in each eye, including large dark and bright crescent-shaped areas on the left and right sides of the blur circle. The nasal edge of the myopic blur circle (viewed through +8 D) appeared brighter than the temporal edge, and the brightness gradient reversed direction in the case of hyperopic blur (temporal edge appeared bright and nasal edge dark through a −8 D lens). This suggests that the peak of the Stiles–Crawford function is decentered to the nasal side of the pupil in both eyes of these subjects. Subject S8 reported the same type of asymmetry in the brightness of the blur-circle for both eyes in the case of myopic focus (+8 D in front of the eye), however, the blur circle appeared uniformly illuminated with the −8 D lens in place (hyperopic focus). The latter response suggests a flat Stiles–Crawford function.

DISCUSSION

All twelve subjects accommodated well in the presence of normal chromatic aberration with mean gain and phase-lag of 0.85 and 90 deg. These measures of gain and phase are similar to data from previous open-loop experiments (Carter, 1962; Stark *et al.*, 1965; Brodkey & Stark, 1967). In monochromatic light gain was reduced by approximately 50% for most subjects (mean = 0.43)

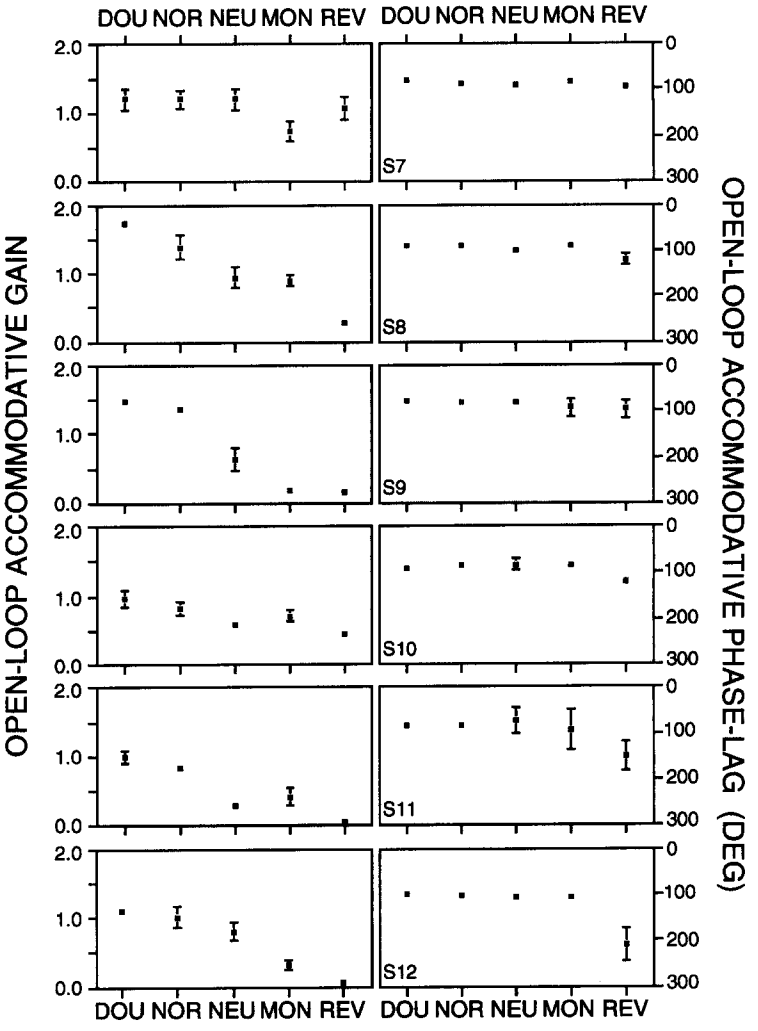

FIGURE 7. Gains (left) and phase-lags (right) for six subjects with high gains (<1.0).

TABLE 2. Gain and phase-lag (deg) of accommodation for subject S4 as negative feedback is reduced in steps from closed-loop (−1.0) to open-loop (0.0) and then positive feedback is increased in steps to +0.4

Feedback	−1.0	−0.5	−0.4	−0.2	0.0	+0.1	+0.2	+0.3	+0.4
Gain	0.40	0.42	0.53	0.56	0.57	0.51	0.40	0.32	0.22
Phase-lag	79	91	110	118	138	102	94	92	98

compared with gain in the normal condition (0.85), but a few subjects responded relatively well in monochromatic light (gain = approximately 0.7). The response in monochromatic light confirms the presence of an achromatic directional stimulus. The effects on dynamic accommodation of doubling, neutralizing and reversing LCA confirm closed-loop findings that both achromatic and chromatic directional signals specify focus of the eye, and that sensitivity to the two aspects of the stimulus varies among individuals (Kruger *et al.*, 1993).

Recently, two investigations used stationary targets instead of sinusoidally moving targets to stimulate accommodation. Bobier *et al.* (1992) used a subjective method to measure accommodation to stationary targets positioned at several stimulus distances between 0 and 6 D, and LCA was altered by special lenses as in the present experiment. Kotulak *et al.* (1995) monitored accommodation continuously while the subject viewed a target positioned at 1 D, and the spectral bandwidth of the illumination was varied to alter the effects of LCA. Both investigators found that LCA had no effect when the target is stationary, and both investigators suggested that there may be separate mechanisms for stationary and moving targets. We have repeated the experiment using stationary stimuli positioned at near (5 D), intermediate (2.5 D) and far (0 D) distances (Kruger *et al.*, 1997). Accommodation was monitored continuously during trials that lasted 40 sec. Subjects accommodated accurately if the target was close to their intermediate resting position *even if LCA was reversed*, but if the target was positioned considerably closer (5 D) or further away (0 D) than the intermediate resting position and LCA was

reversed, subjects had great difficulty bringing the target to focus and maintaining focus for any length of time. The target must be considerably closer or further away than the resting position of accommodation in order to demonstrate the effect of LCA. Kotulak *et al.* (1995) positioned their stationary target at an intermediate distance (1 D) which probably was close to their subjects' tonic resting position of accommodation. Bobier *et al.* (1992) used a subjective method of measuring accommodation (stigmatoscopy) that cannot detect the unstable and erratic accommodative behavior that is evident in continuous recordings of accommodation in monochromatic light and when LCA is reversed (Kruger *et al.*, 1997). With LCA reversed most subjects can maintain focus only for a few seconds, perhaps long enough to align or focus the vernier targets of a subjective optometer; but continuous monitoring of accommodation reveals large oscillations of accommodation, sudden loss of focus, and inaccurate accommodation that is not revealed by subjective measures of accommodation. Our results with stationary targets suggest that the present findings can be extended to static stimulus conditions.

Effect of the lenses on longitudinal chromatic aberration

The measures of LCA made through the three lens doublets (Fig. 3) show that the doubling and reversing lenses alter LCA as intended. However, the simple design of the lenses (zero-power cemented doublets) precludes a perfect correction of LCA by the neutralizing lens. Thus, the neutralizing lens does not entirely eliminate the difference in contrast between spectral components of the retinal image. Reflex accommodation of some subjects is sensitive to very small amounts of LCA (0.25 D) and the residual LCA from the neutralizing lens might have allowed some subjects to accommodate more effectively in the neutralized condition than in the monochromatic condition (Kruger *et al.*, 1995b). Several subjects showed this type of pattern (S3, S4, S7, S9, S12) with higher gain in the neutralized condition than the monochromatic condition.

The doubling lens almost doubles the chromatic difference of focus of the eye, and consequently increases the difference in contrast between spectral components of the retinal image (the hypothesized chromatic stimulus for accommodation). If changing contrast of spectral components of the retinal image drives accommodation, the accommodative response might be enhanced in the doubled condition. Three subjects (S8, S9 and S11) responded with high gain in the normal condition (>1.0) and with even higher gain in the doubled condition, but for most subjects additional LCA did not enhance the response. It seems that a normal amount of LCA is sufficient to stimulate accommodation and additional LCA has no additional effect for most subjects. More important is that the doubled condition did not impair accommodation at all. Thus, the doubled condition serves as a control for the possibility that the reduced response in the neutralized and reversed conditions results from an inadvertently aberrated retinal image.

Finally, the reversing lens effectively reverses the chromatic difference of focus of the eye, and thus reverses the chromatic difference of contrast that specifies focus. Most subjects responded poorly in the reversed condition, one subject (S3) responded with substantial gain in temporal counterphase to the stimulus, and three subjects accommodated in counterphase during some of their trials, although with very low gain (S6, S11, S12). The poor response of most subjects in the reversed condition is in line with the prediction that conflicting chromatic and achromatic signals should counteract each other in the reversed condition.

Effect of the lenses on transverse chromatic aberration

An important consideration is the possibility that the special doublets introduce unwanted aberrations that account for the present results. In particular, if the eye is not well aligned with the special lenses or the Badal optical system, transverse chromatic aberration (TCA) can be introduced. TCA produces a lateral shift in the spatial phase of spectral components of the retinal image, and large amounts of TCA might impair accommodation. Using the present alignment method, mean TCA (six eyes) measured though the Badal stimulus system was 20 arc sec (normal condition in Table 1). This amount of TCA is similar to previous measures, which ranged between +94 and −15 (Simonet & Campbell, 1990) and which generally are <1 arc min (Thibos *et al.*, 1990; Rynders *et al.*, 1995). Thus, the present method of aligning the eye with the artificial pupil did not introduce significant additional TCA. The present alignment method was compared with a subjective method in which the subject positioned their own eye while viewing a red–green vernier target (see Thibos *et al.*, 1990). The two methods provide very similar alignment of the eye, as indicated by the relatively small measures of TCA in the normal condition (Table 1). However, with the special lenses in place, mean TCA increased from +20 arc sec (normal condition), to +47 arc sec (neutralized), to +69 arc sec (doubled), and to +96 arc sec (reversed). The additional TCA induced by the lenses suggests that the lenses were misaligned by a small amount with respect to the achromatic axis of the eye. Perhaps the additional TCA in the neutralized and reversed conditions accounts for the poor accommodative response in those conditions. For example, subject S15 measured 46 arc sec TCA in the normal condition, only 21 arc sec in the doubled condition, twice the normal amount in the neutralized condition (95 arc sec), and three times as much TCA in the reversed condition (122 arc sec). Thus, the increase in TCA in the neutralized and reversed conditions might explain the poor accommodation of this subject in those conditions. However, all the other subjects in Table 1 show more TCA in the doubled condition than the neutralized condition, and one subject (S2) shows twice as much TCA in the doubled condition than the reversed condition. The doubling lens increases TCA but has no effect on reflex accommodation. The strong accommo-

dative response of subjects in the doubled condition argues against the possibility that TCA reduced the response in the neutralized and reversed conditions. In support of this position, the monochromatic condition eliminates both LCA and TCA, yet dynamic accommodation is impaired in monochromatic light. The present measures of TCA are not unusually large (Ogboso & Bedell, 1987; Simonet & Campbell, 1990; Thibos *et al.*, 1990; Rynders *et al.*, 1995) and have little or no effect on the contrast of the 2.7 cpd sine-wave grating target (1 cycle = 22.2 min arc).

The effect of the lenses also was evaluated in experiments that measured contrast sensitivity, contrast-decrement sensitivity, and depth of focus of the eye through the Badal stimulus system. There are essentially no differences in these measures taken through the various lenses (Stone *et al.*, 1990; Mathews *et al.*, 1992; Mathews *et al.*, 1994).

Was feedback eliminated?

Another consideration is whether a small amount of blur feedback might account for the present results. Using the present method of calibration most subjects (approx 80%) under-accommodate by a small amount for the 3 D stimulus distance. This results in a small amount of positive feedback in the nominally open-loop condition (e.g. +0.1). On the other hand, over-accommodation during calibration results in residual negative feedback during the open-loop condition. The control experiments on one of the subjects who responded well in monochromatic light show that residual negative feedback does not account for the open-loop response. If unintended negative feedback (e.g. −0.1) explains the open-loop response, the response should have disappeared when the equivalent amount of positive feedback (e.g. +0.1) was introduced. Instead gain decreased gradually as positive feedback was increased from +0.1 to +0.4, and phase-lag remained between 90 and 100 deg. Positive feedback moves the retinal image in the wrong direction when the eye accommodates appropriately, producing more defocus blur instead of less, and the reduced accommodative gain in the presence of considerable positive feedback (+0.4) is not surprising. The ability of subjects to accommodate in the presence of small amounts of positive feedback in monochromatic light supports the notion of an achromatic directional signal for accommodation. Residual feedback (positive or negative) cannot account for the present results regarding chromatic aberration, or explain the ability of subjects to accommodate in monochromatic light.

It also seems unlikely that the results represent voluntary accommodation or a response to extraneous cues such as lateral target motion or changes in the color appearance of the target. Subjects respond in the open-loop condition over a broad range of temporal frequencies (Carter, 1962; Brodkey & Stark, 1967; Kruger *et al.*, 1995a) and if extraneous cues and voluntary accommodation produce the open-loop response, the response should disappear at higher temporal frequencies (0.6–1.6 Hz). Careful alignment of the optical system and target reduced lateral target motion to approximately 1.5 arc sec, and lateral motion and changes in target color were not evident to the subjects during the experiment. Trained observers cannot identify the color of the changes produced by LCA and defocus (± 1 D) when the target is a 3 cpd perceptually white sine-wave grating viewed through a 3 mm artificial pupil (Kruger *et al.*, 1995a). In the present experiment subjects responded on first exposure to the various stimulus conditions, and they were not conditioned to respond through training or prior experience.

Achromatic and chromatic directional signals specify ocular focus

The majority of subjects accommodated well in the normal and doubled conditions, gain was reduced in the neutralized and monochromatic conditions, and accommodation was poor in the reversed condition. This pattern of behavior has been observed under closed-loop conditions, and is typical of subjects who depend on the chromatic signal for reflex accommodation (Kruger *et al.*, 1993). A few subjects responded in temporal counter-phase to the stimulus during some trials of the reversed condition, suggesting high sensitivity to the chromatic signal combined with low sensitivity to the achromatic signal. Finally, a few subjects responded well under all five stimulus conditions (S4, S8, S10) suggesting high sensitivity to both chromatic and achromatic signals. Despite these individual differences, most subjects responded to both aspects of the stimulus. The results support the hypothesis that both achromatic and chromatic directional stimuli specify ocular focus and drive reflex accommodation.

In monochromatic light, decentered pupils and asymmetric monochromatic aberrations (spherical aberration and coma) are the most likely source for an *optical* signal that specifies focus. In the present experiment an attempt was made to minimize or eliminate these optical factors by imaging a 3 mm artificial pupil in the subject's pupil plane, close to the visual achromatic axis of the eye. The measures of transverse chromatic aberration taken through the optical system (Table 1) suggest that the center of the artificial pupil was positioned close to the achromatic axis of the eye, because a decentered artificial pupil would have introduced larger amounts of TCA in the normal condition. The present experiment cannot rule out the possibility that a small amount of asymmetric monochromatic aberration was present, but it is unlikely that aberrations (coma) or a decentered pupil account for the large response of some subjects in monochromatic light.

This leaves the possibility that the small acceptance angles of cones (Stiles–Crawford effect) play a role, perhaps as described in the Introduction. Three subjects responded particularly well in monochromatic light and were recalled to determine whether a highly decentered Stiles–Crawford effect might explain their accommodative ability. Using the method of entoptic viewing, two subjects (S4 and S10) described a markedly asymmetric

Stiles–Crawford function, with the foveal cones pointing to the nasal side of the pupil in both eyes. One of these subjects (S4) is highly myopic (−7 D) and is like several of the subjects examined by Westheimer (1968) who had markedly decentered Stiles–Crawford functions, both by the method of entoptic viewing as well as by standard psychophysical testing. Subject S4 is deuteranomalous and responds relatively poorly to the effects of LCA. Subject S10 is less myopic (−0.75 D) but also described a pronounced nasal decentration of the Stiles–Crawford function. Subject S8 is emmetropic and described an asymmetric blur circle when focus was in front of the retina (+8 D), suggesting nasal decentration of the Stiles–Crawford function, however, the subject described a uniformly illuminated blur circle when focus was behind the retina (−8 D), suggesting a flat Stiles–Crawford function. It is important to note that there also are subjects who describe asymmetric blur circles but who do not accommodate well in monochromatic light (e.g. S1). The issue is complicated further because coma also produces asymmetric blur circles (Howland & Howland, 1977; Campbell *et al.*, 1990; Artal *et al.*, 1995). The present method of viewing blur circles entoptically used natural pupils (5–7 mm) that were larger than the 3 mm artificial pupil used in the accommodation experiment. Thus, the asymmetric intensity patterns that were viewed entoptically could have included the effects of asymmetric monochromatic aberrations that were not present during the accommodation experiment. Asymmetric aberrations can interact with a decentered Stiles–Crawford effect to increase or decrease the perceived asymmetry of blurred images (Ye *et al.*, 1992; Rynders *et al.*, 1995), and this might explain why subject S8 described an asymmetric blur circle for myopic focus but a symmetric intensity distribution for hyperopic focus.

The method suggested above (decentered Stiles–Crawford function) relies on large numbers of cone receptors, all facing toward a common eccentric pupillary point, and acute sensitivity to small changes in spatial phase. The method seems unlikely for a 2.7 c/d sine grating oscillating at the relatively low temporal frequency of 0.2 Hz. Another possibility is that some receptors or groups of receptors sample light from circumscribed areas of the pupil (Westheimer, 1967; Heath & Walraven, 1970; Bailey & Heath, 1978; Williams, 1980). Foveal cones that face the nasal edge of a 3 mm pupil receive light from the temporal edge of the pupil at an angle of approximately 8 deg to the axis of the cone. This is larger than estimates of the half-acceptance angle of individual cones, which could be as small as a few degrees (Enoch & Tobey, 1981). Sampling signals from opposite sides of the pupil is the basis of Scheiner's principle and the Foucalt knife edge test for determining the focal point and wavefront aberration of optical systems. If some foveal cones sample from opposite sides of the pupil (e.g. Williams, 1980), comparison of cone responses as blurred edges move across the fovea could provide a sensitive measure of defocus.

The stimulus from chromatic aberration has received considerable interest and investigation over several decades (Fincham, 1951; Crane, 1966; Troelstra *et al.*, 1964; Stark & Takahashi, 1965; Smithline, 1974; Phillips & Stark, 1977; Charman & Tucker, 1978; Wolfe & Owens, 1981; Kruger & Pola, 1986; Lovasik & Kergoat, 1988; Switkes *et al.*, 1990; Flitcroft, 1990; Kergoat & Lovasik, 1990; Bobier *et al.*, 1992; Kruger *et al.*, 1993; Kotulak *et al.*, 1995; Aggarwala *et al.*, 1995). Of fundamental importance is the conception by Crane (1966) that chromatic difference of focus (LCA) allows L-, M- and S-sensitive-cone classes to analyze the retinal image simultaneously in three focal planes. If early visual processing (edge detection) is performed separately by cone class, a comparison of signals could provide a measure of defocus. Signals that might reliably indicate focus include the position of *spatial primitives* such as the peaks, centroids and zero-crossings in the second derivative of the retinal intensity distribution, and the *contrast* of the image. Previous investigators have described the effects of LCA as color fringes at luminance borders (Fincham, 1951; Crane, 1966) and recently as the hue and saturation at the peaks and troughs of spatial sine-wave gratings (Kruger *et al.*, 1995a). However, the chromatic stimulus can be described simply as contrast ($L_{max} - L_{min}/L_{max} + L_{min}$) measured separately for different spectral components (e.g. red, green, blue) of the retinal image. The Michelson formula takes into account both the peaks (L_{max}) and troughs (L_{min}) of the grating, and focus is specified by comparing contrast rather than by measuring chromaticity. Figure 8 illustrates the effects of defocus and LCA on the contrast of three spectral components of a 2.7 c/d white sine-wave grating viewed through a 3 mm pupil, as in the present experiment. Focus of the eye is specified with reference to 525 nm light, and red (610 nm) and blue (465 nm) spectral components come to focus approximately 0.5 D on either side of the green (525 nm) component. The three curves illustrate how the contrasts of narrowband

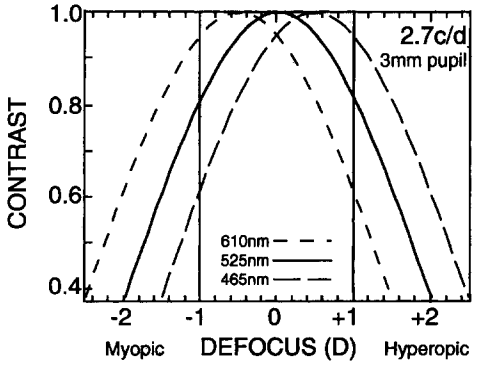

FIGURE 8. Contrast for three monochromatic spectral components (465 nm, 525 nm and 610 nm) of the retinal image of a white 2.7 c/d sine-wave grating viewed through a 3 mm pupil as a function of defocus behind and in front of the retina. Defocus is referenced to 525 nm light. The red (610 nm) and blue (465 nm) components focus approximately 0.5 D on either side of the green (525 nm) component of the image.

red, green and blue components of the retinal image change as focus moves behind and in front of the retina. Over-accommodation (−1 D) is characterized by higher contrast for the long-wavelength component of the image than for the middle and short-wavelength components, and under-accommodation (+1 D) by higher contrast for the short-wavelength component than for the middle and long-wavelength components. At 2.7 c/d, defocus in the amount of 1 diopter (with reference to 525 nm) produces a chromatic difference in contrast of up to 20% between spectral components that are focused 0.5 D apart. The order of contrasts reverses from red > green > blue to red < green < blue as focus changes from myopic to hyperopic. In the present experiment the target grating was illuminated by broadband white light from a tungsten-halogen source that provided a continuous spectrum (3000 K) of illumination, and Fig. 8 only illustrates the effects of defocus on three narrowband spectral components of the retinal image. Following this type of model, ocular focus can be specified by cone-contrast measured separately by L-, M- and S-sensitive-cone classes (Kruger *et al.*, 1995a). The present result supports the hypothesis that the relative contrast of spectral components of the retinal image specifies ocular focus and drives reflex accommodation.

These findings may have implications for the process of emmetropization, in which growth and development of the optical components of the eye are coordinated to minimize ametropia. There is agreement that an in-focus retinal image is important for emmetropization (Rabin *et al.*, 1981; Wallman, 1993; Smith *et al.*, 1994) but the optical signals that specify focus of the eye remain obscure. Bartmann & Schaeffel (1994) suggest that the system monitors luminance contrast over long periods of time to determine focus, and that luminance contrast provides the optical stimulus for emmetropization. This model follows the standard view that luminance contrast provides the primary stimulus for reflex accommodation and that feedback is an essential part of the process. Considering the remarkable sensitivity of the visual-accommodative system to the effects of LCA, and the possibility that the vergence of light might drive accommodation, it would be a mistake to overlook the effects of aberrations as optical stimuli for emmetropization, and the possibility that the process is mediated by the waveguide nature of cones. Sensitivity to the monochromatic and polychromatic aspects of dioptric blur varies broadly among the population, and some subjects seem to lack sensitivity to one or both aspects of dioptric blur (Gwiazda *et al.*, 1993, 1995; Kruger *et al.*, 1995). Individuals may be at risk for the development of ametropia if they lack part or all of the sensory apparatus for monitoring focus of the eye.

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